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THE GENUS *TILIA* IN OHIO*

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Examination of about 250 Ohio specimens of *Tilia* shows that the Ohio population consists of three basic species (*americana* L., *heterophylla* Vent., *floridana* [V. Engler] Small) and a species-complex here referred to as *T. neglecta* Spach.

T. americana varies considerably; the limits of the taxon are obscure, not only in Ohio, but through much of its range. However, in the northwestern part of its range, in Minnesota, the species seems more stable than elsewhere; little variation was observed upon examination of a considerable number of specimens (in University of Minnesota herbarium). Some Ohio specimens resemble those of this northwestern population; others suggest introgression from some other species, probably *heterophylla*. The glacial and postglacial history of *Tilia* furnishes a clue to the explanation.

At the time of the last (Wisconsin) ice maximum, *Tilia* survived only beyond the ice margin—in the Driftless Area of Wisconsin, a great re-entrant angle between glacial lobes; on the northern Appalachian Upland; and elsewhere in front of the ice border, which lay across Indiana and Ohio. In its postglacial migration, as indicated by pollen analysis of bogs (Sears, 1942), *Tilia* appeared early in what is now the northwestern part of its range, earlier than (with few exceptions) in the central part of its range (Indiana, Ohio). These locations of early entry into Ohio and Indiana are north of bogs whose records show later entry, and are near the periphery of the Prairie Peninsula. This suggests spread from a refugium in Wisconsin (and possibly farther to the southwest), spread not only westward, but also southeastward. This *Tilia* population had not come in contact with other taxa, hence is the least variable and the true basic species (even if it does not coincide with a taxonomic type).

Comparison of Ohio material with northwestern material shows that some specimens resemble the more northwestern ones. These are shown on the map (fig. 2 A) by dots with an upright appendage, and are here considered to represent the basic species, uncontaminated by other species (fig. 1 A). Many other specimens are sufficiently similar to be placed in the same taxonomic "pigeon-hole"; these are shown by dots on the map. Still others are generally referred to *T. americana*, but depart in one or more characters from the basic taxon; these are shown by circles on the map. *T. americana* (inclusive) is, in Ohio, almost confined to the area of Wisconsin glaciation.

T. heterophylla (fig. 1 B) is found in unglaciated Ohio and the dissected border of Illinoian glaciation (fig. 2 B). It is a characteristic species of the Mixed Mesophytic climax association, occurring abundantly in that association in the Cumberland Mountains and Cumberland Plateau and in coves of the Great Smoky

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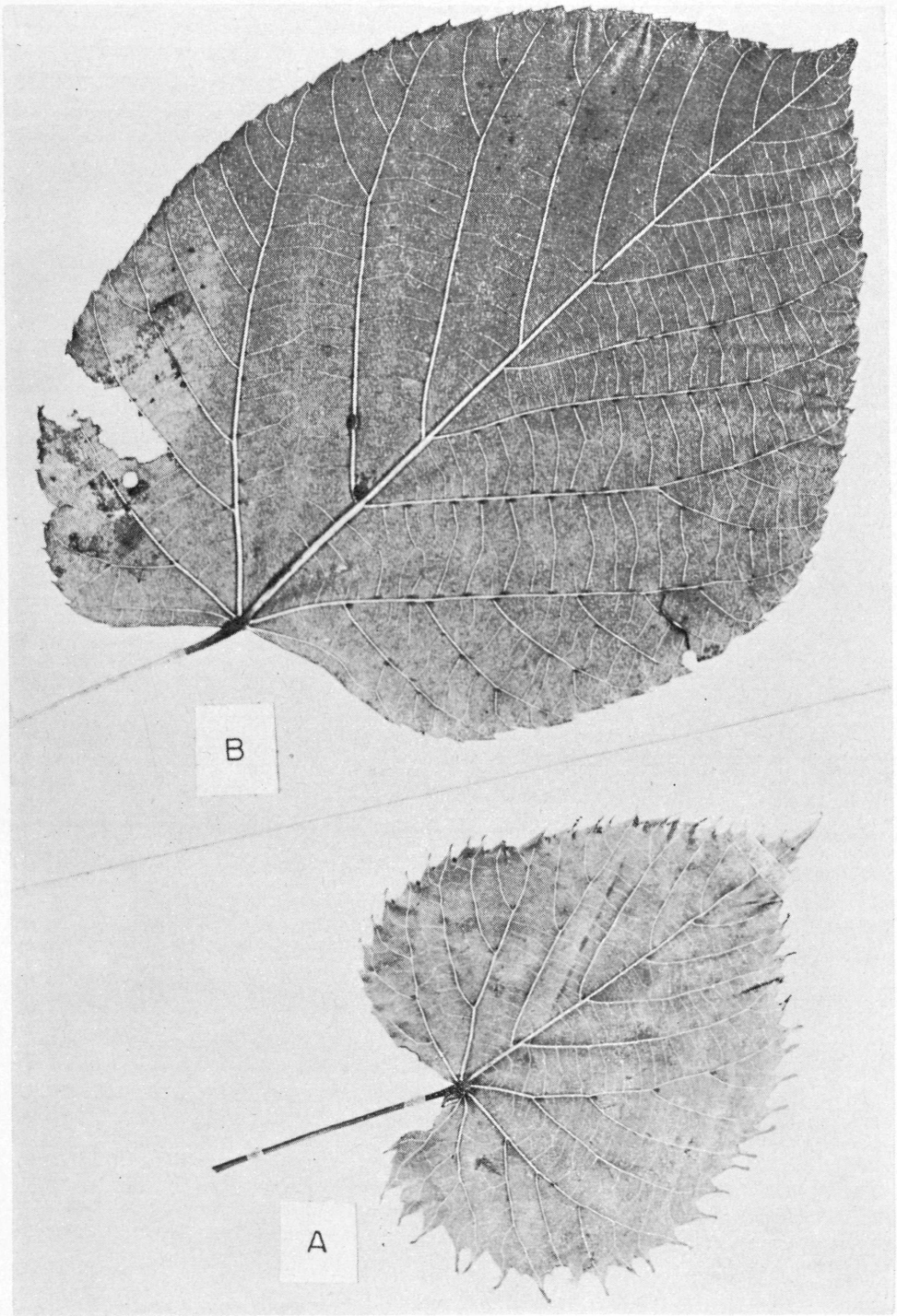

FIGURE 1. A, Leaf of *T. americana*. B, Leaf of *T. heterophylla*, natural size. (From photostats of pressed leaves.)

Mountains. An abundant species of the old (ancestral) area of deciduous forest, and probably by Pleistocene time almost confined to the Appalachian Highland, its range later must have been curtailed on the north by Pleistocene ice. *T. floridana*, represented by a few specimens from unglaciated eastern Ohio, may have

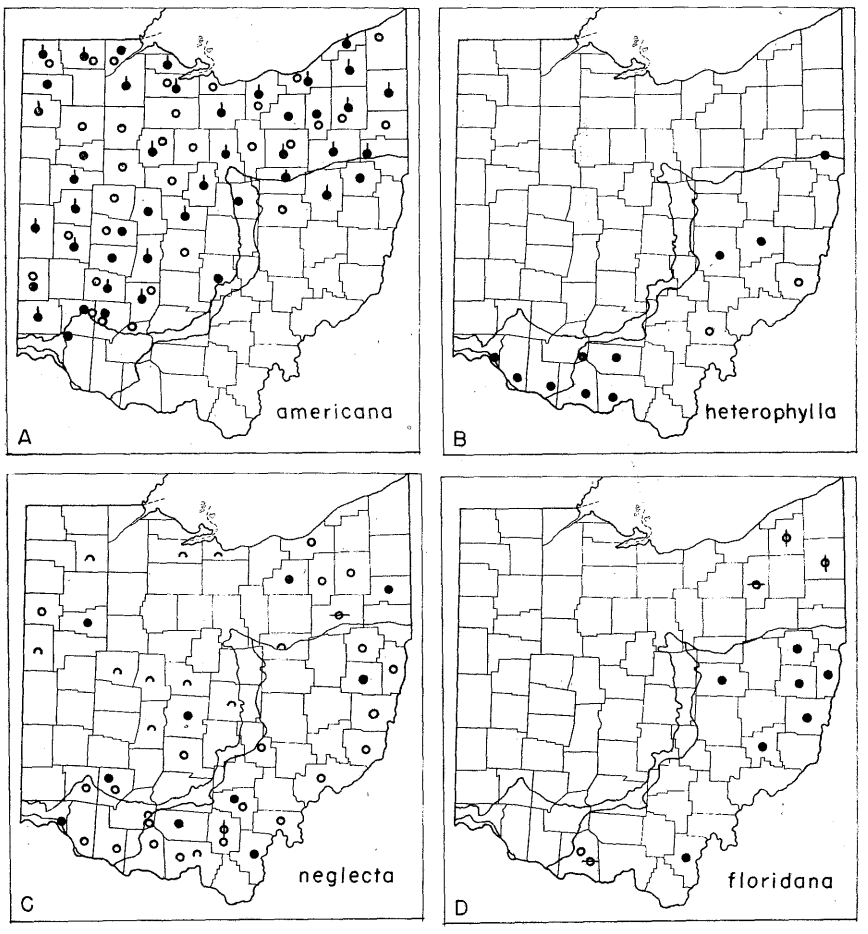

FIGURE 2. A, B, C, D. Distribution of four species of *Tilia* in Ohio.

had a similar history. Along a tension zone south of the Wisconsin ice, unlike races of *Tilia* met and mixed, resulting in introgression from *T. heterophylla* (and probably *T. floridana*) into the more northern *T. americana*.

In order to analyze variation as displayed by the Ohio population of *Tilia*, pictorialized scatter-diagrams of the type devised by Anderson (1949, 1952, 1953) have been constructed (fig. 3). For plotting *americana*, only specimens representing the "basic species" were used. The glyphs of this species occupy a definite and circumscribed area on the diagram, and are far-removed from those of *heterophylla*. Glyphs of a third "species" or "species-complex," *T. neglecta*, occupy an

intermediate position, overlapping in position those of *americana* and *heterophylla*.

Basic *T. americana* may be recognized by three leaf characters: leaves glabrous beneath, with axillary tufts at primary veins, rarely at secondary veins; large jagged teeth usually 3–5 mm high; few teeth per unit length, 3–5 in 2 cm of leaf margin. *T. heterophylla* differs markedly in these three characters: leaves densely pubescent beneath with matted branched hairs, axillary tufts present but usually not conspicuous; teeth low, less than 2 mm high; more teeth per unit length, usually 6–8 or more in 2 cm of leaf margin. *T. neglecta*, as here used, lacks such definite characters; leaves vary from almost glabrous to thinly pubescent with

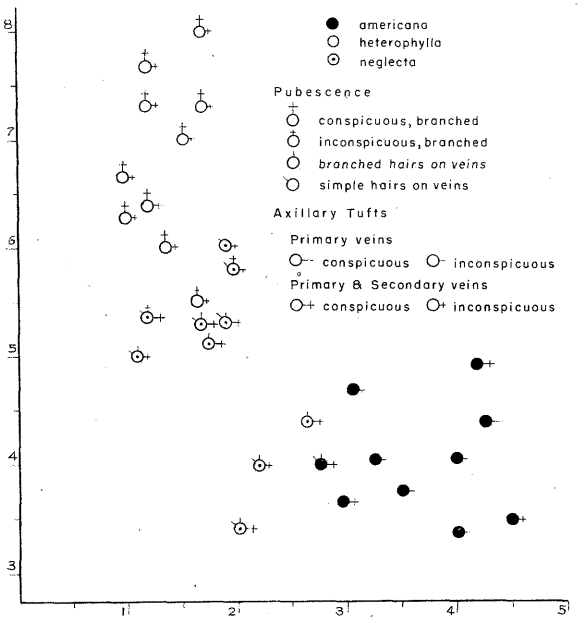

FIGURE 3. Pictorialized scatter-diagram of Ohio population of *Tilia americana*, *heterophylla*, and *neglecta*, based on leaf characters. Horizontal axis: height in mm of upper (apical) edge of teeth. Vertical axis: number of teeth per 2 cm of leaf margin. Glyph appendages indicate pubescence and axillary tufts; differences in length relate to intensity of character depicted.

simple or branched hairs or both; axillary tufts usually prominent; teeth vary in size, shape, and in spacing. In certain characters, it resembles *americana*, in others, *heterophylla*. Features of the glyphs and their positions indicate that *T. neglecta* has arisen postglacially as a result of contact between *americana* and *heterophylla*.

Distribution of *T. neglecta* (dots on map), of specimens doubtfully referred to *neglecta* (circles on map), and of those which might equally well be thought of as *americana* in part (half-circles on map), shows this complex (fig. 2 C) to be most abundantly represented near the zone of contact of *heterophylla* and *americana*, but present also farther north well within the range of *americana*. Hybridization and backcrossing with *americana* have carried introgression far northward. Occa-

sional specimens have characters suggesting *heterophylla* (horizontal line through circle) or *floridana* (vertical line through circle).

In some local areas just outside the glacial boundary, variation in the *Tilia* population suggests hybrid swarms. Such is the case with the *Tilia* population in Fort Hill State Memorial, Highland County, where some specimens are definitely referable to *T. heterophylla*, some doubtfully to *T. americana*, and others to *T. ngelecta*. The scatter-diagram (fig. 4) shows the glyphs scattered from within the area of *americana* glyphs of fig. 3 to within the area of *heterophylla* glyphs, with most in the intermediate position of *T. neglecta*.

T. floridana (fig. 2 D) seems to have played a lesser part in the variation of *Tilia* in Ohio. A few specimens suggest admixture with *heterophylla* (horizontal

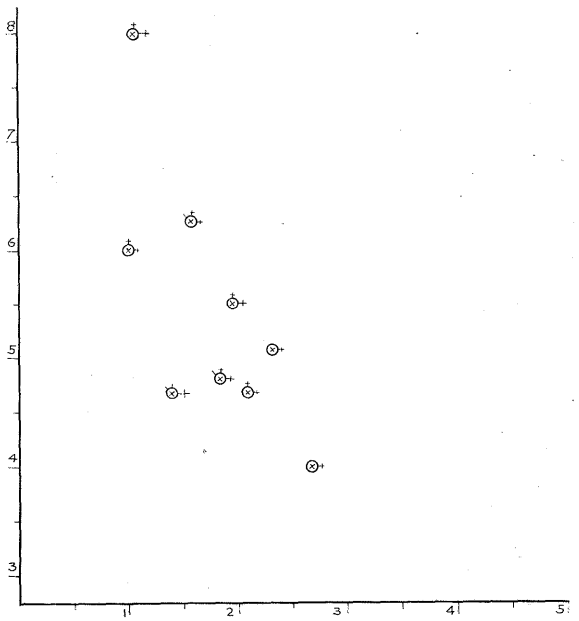

FIGURE 4. Pictorialized scatter-diagram of *Tilia* population of Fort Hill, Highland County. Axes and glyph appendages as in figure 3.

line through circle), a few (from the northern part of the Allegheny Plateau) with *americana* (vertical line through circle). It is so poorly represented, numerically, that no analysis is possible. The leaves are coarsely toothed as in *americana*; but the almost imperceptible pubescence of the lower leaf-surface, which imparts a velvety feel even when the leaves appear glabrous, will distinguish it from other species.

A key for the identification of these species of *Tilia* as seen in Ohio will be found in "The Woody Plants of Ohio" (Braun, 1960, Ohio State University Press).

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